

Using GIS to relate small mammal abundance and landscape structure at multiple spatial extents: the northern flying squirrel in Alberta, Canada

MATTHEW WHEATLEY,* JASON T. FISHER,† KARL LARSEN,‡
JOSEPH LITKE§ and STAN BOUTIN¶

*Department of Biology, University of Victoria, Box 3020 STN CSC, Victoria, British Columbia, Canada V8W 3N5;

†Alberta Research Council, PO Bag 4000, Vegreville, Alberta, Canada T9C 1T4; ‡Department of Natural Resource

Sciences, Thompson Rivers University, Box 3010, Kamloops, British Columbia, Canada V2C 5N3; §Fiera Biological

Consulting Ltd, PO Box 988 Rocky Mountain House, Alberta, Canada T4T 1A7; and ¶Department of Biological

Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E9

Summary

1. It is common practice to evaluate the potential effects of management scenarios on animal populations using geographical information systems (GIS) that relate proximate landscape structure or general habitat types to indices of animal abundance. Implicit in this approach is that the animal population responds to landscape features at the spatial grain and extent represented in available digital map inventories.

2. The northern flying squirrel *Glaucomys sabrinus* is of particular interest in North American forest management because it is known from the Pacific North-West as a habitat specialist, a keystone species of old-growth coniferous forest and an important disperser of hypogeous, mycorrhizal fungal spores. Using a GIS approach we tested whether the relative abundance of flying squirrel in northern Alberta, Canada, is related to old forest, conifer forest and relevant landscape features as quantified from management-based digital forest inventories.

3. We related squirrel abundance, estimated through live trapping, to habitat type (forest composition: conifer, mixed-wood and deciduous) and landscape structure (stand height, stand age, stand heterogeneity and anthropogenic disturbance) at three spatial extents (50 m, 150 m and 300 m) around each site.

4. Relative abundances of northern flying squirrel populations in northern and western Alberta were similar to those previously reported from other regions of North America. Capture rates were variable among sites, but showed no trends with respect to year or provincial natural region (foothills vs. boreal).

5. Average flying squirrel abundance was similar in all habitats, with increased values within mixed-wood stands at large spatial extents (300 m) and within deciduous-dominated stands at smaller spatial extents (50 m). No relationship was found between squirrel abundance and conifer composition or stand age at any spatial extent.

6. None of the landscape variables calculated from GIS forest inventories predicted squirrel abundance at the 50-m or 150-m spatial extents. However, at the 300-m spatial extent we found a negative, significant relationship between average stand height and squirrel abundance.

7. *Synthesis and applications.* Boreal and foothill populations of northern flying squirrel in Canada appear unrelated to landscape composition at the relatively large spatial resolutions characteristic of resource inventory data commonly used for management and planning in these regions. Flying squirrel populations do not appear clearly associated with old-aged or conifer forests; rather, they appear as habitat generalists. This study suggests that northern, interior populations of northern flying squirrel are probably more related to stand-level components of forest structure, such as food, microclimate

(e.g. moisture) and understorey complexity, variables not commonly available in large-scale digital map inventories. We conclude that the available digital habitat data potentially exclude relevant, spatially dependent information and could be used inappropriately for predicting the abundance of some species in management decision making.

Key-words: geographical information systems, *Glaucomys*, habitat type, landscape composition, predictive modelling

Journal of Applied Ecology (2005) **42**, 577–586

doi: 10.1111/j.1365-2664.2005.01034.x

Introduction

Habitat structure and the juxtaposition of suitable and unsuitable habitats are known to affect the distribution of forest vertebrates (Rodríguez & Andrén 1999; Bowman, Forbes & Dilworth 2000; Reunanen *et al.* 2002). An understanding of relationships between animal distribution, habitat types and landscape patterning is of considerable importance in applied ecology, where management actions (e.g. forest harvesting) necessarily alter patch size, connectivity and age distribution of habitats. Predictive models that describe relationships between animal populations and spatial habitat structure are commonly generated using Geographic Information Systems (GIS) (Verner, Morrison & Ralph 1986; Mackey & Lindenmayer 2001; Arbuttle & Downing 2002; Rowe *et al.* 2002; Hatten & Paradzick 2003; Gibson *et al.* 2004), which are used to evaluate species-specific responses to habitat heterogeneity and quantify the spatial extent (Kotliar & Wiens 1990) at which a species uses or selects for landscape features (Johnson, Seip & Boyce 2004). Once quantified, responses can be modelled using GIS-based techniques such as Spatially Explicit Population Dynamic Models, which predict animal distributions based on the interaction between individual behavioural processes and landscape structure (Rushton *et al.* 1997; Rushton *et al.* 2000). These methods have become common for sustainable land management strategies, and increasingly form the basis for species–habitat management activities (Rushton, Ormerod & Kerby 2004).

Digital GIS-based land cover inventories allow for efficient quantification of landscape structure at relatively large spatial extents (i.e. above forest stand level; Jaberg & Guisan 2001; Osborne, Alonso & Bryant 2001; Pearce *et al.* 2001; Suárez-Seoane, Osborne & Alonso 2002; Holloway, Griffiths & Richardson 2003; Jeganathan *et al.* 2004) but their usefulness for animals that potentially respond to fine-scale habitat features can be limited because such high-resolution data are rarely incorporated into relatively large regional or provincial digital inventories (Engler, Guisan & Rechsteiner 2004). For management areas that rely heavily on digital forest inventories in decision-making processes, such as many North American forestry operations, understanding which animals respond to landscape features available

on GIS is key for effective and sustainable planning. Animals considered ‘habitat specialists’ are of particular interest in such a predictive modelling context, because of their potential inability to tolerate significant changes in structural or spatial habitat attributes generated from management activities (Bright 1993). However, habitat features that define the functional landscape (Kotliar & Wiens 1990; Johnson, Parker & Heard 2001) and affect a species’ distribution must be quantifiable and measurable at a relevant spatial extent on the GIS before this can be an effective approach (Levin 1992; Turner & Gardner 1991; Turchin 1996).

The northern flying squirrel *Glaucomys sabrinus* Shaw has become of particular interest to forest management in the USA and Canada (Carey 1995, 2000; Smith & Nichols 2003) because of its direct relationship with old-growth forest and the fungal communities therein. Essential to the growth of woody vegetation is its symbiotic relationship with nitrogen-fixing hypogeous mycorrhizal fungi: the fungi associate with roots and provide essential nutrients for tree growth, an obligatory relationship for both trees and fungi (Claridge, Cork & Trappe 2000). Generally, neither mycorrhizal fungi nor their hosts complete their life cycle independently (Maser, Trappe & Nussbaum 1978). Because the fungi are hypogeous (i.e. completely underground), they lack above-ground fruiting bodies and rely completely on animals for spore dispersal, primarily microtines and tree squirrels (North, Trappe & Franklin 1997; Carey *et al.* 1999). Flying squirrels feed almost exclusively on hypogeous fungi (Maser *et al.* 1986; Currah *et al.* 2000) and, unlike microtines, disperse the spores through faecal deposits at spatial extents greater than the stand level. The flying squirrel is considered to be a habitat specialist and, through its fungal relationships, a ‘keystone’ species of mature, coniferous forest (Maser, Trappe & Nussbaum 1978; Smith & Nichols 2004). As a cavity nester and prey species for many predators (including threatened owl species; Carey, Horton & Biswell 1992), the presence of flying squirrels has been linked to old-growth coniferous forests and is considered to reflect ecosystem health (Carey 2000).

It is because of this link to old-growth forests that the majority of research on the flying squirrel comes almost exclusively from forests in the Pacific North-West of North America (Maser, Trappe & Nussbaum 1978;

Carey 2000; Ransome & Sullivan 2003; Smith & Nichols 2003), with reference to prey availability and recovery efforts for threatened northern spotted owls *Strix occidentalis* Merriam (Carey 1995). However, the Pacific North-West is considerably different in climate and both physical and spatial forest structure compared with forests composing the remainder and majority of the flying squirrel's natural distribution (i.e. boreal Canada and interior Alaska). Consequently, flying squirrel habitat associations are not known throughout most of its northern range (but see McDonald 1995), particularly in the foothills and boreal regions of Canada where industrial development is increasingly widespread. Flying squirrels appear to be associated with mature, conifer forest attributes directly altered by contemporary, multi-pass forest harvesting (e.g. stand age, snag retention and understorey development; Carey 1995). This is a problematic association, and a key industrial concern in northern and western Alberta, where harvest rotation age is commonly less than the average and natural ages of mature and old forests. Through rotational harvesting over time, forest patches become younger in age and smaller in size.

The focus of this study was to relate flying squirrel abundance to parameters of forested landscape typically assessed and readily available via remote sensing using management-based GIS inventories. Our objectives were to (i) compare squirrel abundance among broad habitat categories based on conifer and deciduous composition, and (ii) relate observed flying squirrel abundance to landscape structure around each sampling area at three spatial extents (300 m, 150 m and 50 m). We predicted that (i), based on this species' previously described association with old conifer forests and stand-level forest attributes (Carey 1995; McDonald 1995), flying squirrel abundance would be positively associated with conifer composition, stand height and stand age, and negatively associated with younger mixed-wood stands dominated by a deciduous canopy; and (ii), based on previous research suggesting stand-level associations between northern flying squirrels and habitat variables, any relationships regarding squirrel abundance would be found with landscape variables quantified at small spatial extents. To explore this we sampled northern flying squirrels within a range of conifer-dominated and deciduous-dominated forest types, from across northern and west-central Alberta.

Materials and methods

STUDY AREAS AND SITE SELECTION

Study location

This study combined results from two initially separate, partially co-ordinated projects. Both employed identical live-trapping techniques and were pooled together here in one study. There were slight differences in sampling

year and transect length among areas, but we accounted for these differences statistically and through capture per unit effort standardizations (see the Statistical Analyses). Sampling was conducted across northern and west-central Alberta, Canada, within the boreal mixed-wood and the foothills natural ecoregions (Strong 1992). Twenty-three sites were sampled in the boreal ecoregion: three near Fort McMurray (56°N, 111°W), three near Lac La Biche (53°N, 112°W), three near Athabasca (55°N, 114.5°W), eight near Manning (57°N, 118°W) and six near Grande Prairie (55°N, 119°W). Nine sites were sampled in the foothills ecoregion near Hinton (53°N, 117°W).

The boreal ecoregion of Alberta is a heterogeneous mixture of forest stands, including trembling aspen *Populus tremuloides* Michx., white spruce *Picea glauca* Moench and jack pine *Pinus banksiana* Lamb. dominating upland areas, and stands of black spruce *Picea mariana* Mill., larch tamarack *Larix laricina* K. Koch., white birch *Betula papyrifera* Marsh. and balsam poplar *Populus balsamifera* L. dominating lowland areas. Extensive black spruce bogs, larch tamarack bogs and peatland are common in lowland areas. Stand age is a mixture of young forest (< 20 years) of both fire and harvest origin, and mature and old-growth forest (> 20–100+ years) of fire origin. Both anthropogenic and natural disturbance features are widespread. Fire is the primary disturbance pattern, followed by extensive oil and gas seismic exploration and active forest harvesting. The general topography is undulating to level.

The forest canopies of deciduous-dominated stands consisted primarily of mature to old trembling aspen, with average stand ages ranging from 62 to 107 years, and with understorey shrub species including wild rose *Rosa* spp. (Moss 1994), alder *Alnus crispa* Pursh and hazel *Corylus cornuta* Marsh. Deciduous snags in various stages of decay were numerous within these stands. Mixed-wood stands had trembling aspen-dominated canopies with roughly 40% white spruce, and a spruce-dominated subcanopy with deciduous snags was common. Dense understoreys consisted of rose, alder, hazel, cranberry *Viburnum* spp. (Moss 1994), saskatoon *Amelanchier alnifolia* Nutt. and honeysuckle *Lonicera* spp. (Moss 1994). Mixed-wood canopy trees on average ranged from 61 to 103 years old. Conifer-dominated stands consisted primarily of mature white spruce (60–70% of canopy), averaging 67–111 years of age, mixed with mature trembling aspen (< 25%). Immature understorey species included trembling aspen, balsam poplar, lodgepole pine *Pinus contorta* London and alder all in low abundance. These stands had willow *Salix* spp. (Moss 1994) and bunch berry *Cornus Canadensis* L. at low densities in the understorey, with dense coverage of labrador tea *Ledum groenlandicum* Oeder and mosses *Sphagnum* spp. (Ireland 1980). These stands contained many conifer snags and large coarse woody debris.

Within the boreal ecoregion we established five study sites (sites 1–5; Fig. 1) and trapped flying squirrel in three of the most common forested habitats found

within each (24 boreal sampling transects total). We sampled in deciduous-dominated stands (primarily trembling aspen), deciduous–conifer mixed-wood stands (trembling aspen mixed primarily with white spruce and to a lesser extent larch tamarack) and conifer-dominated stands (primarily white spruce). Live-trapping areas were established in mature and old forests that previously had not been logged.

Foothills ecoregion

The foothills ecoregion of Alberta consists of foothills running north-west to south-east along the front range of the Rocky Mountains. The topography is moderate to steep, with elevation ranging from 1200 m to 1600 m. Coniferous forest, 80–120-year-old *Pinus contorta* London (*Picea glauca*, *Picea mariana* and *Abies* spp.; Moss 1994), covers more than 80% of the area; smaller proportions of both younger and older stands, of both fire and logging origin, are dispersed throughout. Within the study area, large patches of mature lodgepole pine, white spruce and mixed lodgepole pine–white spruce could be found.

Deciduous-dominated stands were similar in composition and age to those described for the boreal ecoregion. Lodgepole pine stands were the dominant feature within the foothills landscape (roughly 80% by area). These stands consisted of > 70% lodgepole pine with an understorey composition of alder, wild rye *Elymus* spp. (Moss 1994), labrador tea and mosses (*Ptilium* and *Sphagnum* spp.; Ireland 1980). Black spruce occupied a portion of the canopy, but at low densities. Immature white spruce and fir *Abies balsamea* L. were present at low densities. Standing and burnt snags were common features within pine stands. Spruce–fir stands consisted of roughly 30% spruce and < 70% fir (*Abies lasiocarp* Hook. and *Abies balsamea*). The understorey was composed of sapling fir, feather moss *Hylocomium* spp. (Ireland 1980) and wintergreen *Pyrola* spp. (Moss 1994). Dense alder patches and lichens (*Alectoria*, *Brioria* and *Usnia* spp.; Kershaw, Pojar & Mackinnon 1998) were common in all spruce–fir stands.

Within the foothills ecoregion we established nine sampling transects distributed evenly within three of the most common habitat types: deciduous-dominated (trembling aspen), lodgepole pine (> 70% pine) and mixed white spruce–fir. All sites were established in mature forest 95–181 years of age that previously had not been logged.

Site selection

Study sites were selected using a stratified approach to encompass dominant landscape composition and natural heterogeneity for each area, including the most common habitat types by area and their associated disturbance levels. Flying squirrels are known to key into mature forest attributes (e.g. cavities and snags), thus we focused our efforts on stands > 60 years of age. Relative overstorey composition was assessed using

Alberta Vegetation Inventory (AVI) maps, provincial government maps noting all forest polygons, including the stand density, age of origin and dominant tree species assessed and digitized from 1 : 50 000 orthogonal aerial photographs. Site selection criterion included primary and secondary canopy species composition (common, representative of the area or of management concern), stand age (> 60 years of age), intersite proximity (spatially independent) and access.

SAMPLING TECHNIQUES

Flying squirrels were sampled using live-trapping transects, and relative abundance was calculated as captures of unique animals per trap unit effort.

There were eighteen transects sampled near Ft McMurray, Lac La Biche, Athabasca and Hinton (nine boreal, nine foothill) that were 1 km in length, each with 25 trapping stations placed at 40-m intervals. These were plotted to fit patch shape. Some were not straight lines, but transect direction was limited to 60 degrees of the original bearing. If seismic lines or roads were crossed, the width of the intersection was excluded from the transect length.

Fourteen transects were established near Manning and Grande Prairie consisting of two types. Six of these transects were straight lines, 450 m in length. The remaining eight transects consisted of two 200-m parallel transects (100 m apart) but within the same stand. In all cases trapping stations were flagged at 50-m intervals so that 10 trapping stations were established on all transects or pairs therein.

At each trapping station, two live traps (Model 201 or 102, Tomahawk Live Trap Company, Tomahawk, WI) were set: one on the ground at the base of a tree (diameter at breast height > 30 cm), and one in a tree > 1 m but < 2 m above ground. The latter was attached to the trunk using aluminium nails. Rain covers (light plywood or plastic attached with elastic bands) covered at least half of the top and bottom of each trap and a handful of raw cotton or synthetic insulation was placed within. Both traps were placed within 10 m of the trapping station. We pre-baited for at least 4 days prior to setting traps by placing small amounts of peanut butter (< 1 g) on the top of each trap or at the base of flagged trap station trees.

Traps were baited with peanut butter and sunflower seeds, set between 18:00 h and 22:00 h, and checked the next morning between 06:00 h and 11:00 h for 4–7 consecutive nights depending on the study area. Captured animals were marked with either Monel No. 1 eartags (National Band and Tag Co., Newport, KY) or dorsally with non-toxic, permanent ink. Our intent was to record the number of new captures per trapping effort; unique markings were not necessary. For Athabasca, Lac La Biche and Fort McMurray, trapping occurred from 10 June to 3 July 1997. For Grande Prairie and Manning, trapping occurred from 15 June to 15 July 2001. For Hinton, trapping occurred from 17 June to 19 July 2003.

When calculating the number of trap nights, a correction factor of half a trap night was subtracted for each trap found triggered without an animal (Nelson & Clark 1973). No sampling areas were resurveyed between years.

LANDSCAPE COMPOSITION

We quantified habitat around trapping transects by digitally capturing all mapped polygon features within 50 m, 150 m and 300 m around the transect lines. Thus, GIS plots were long and narrow, centred on the transect, and encompassed natural heterogeneity within sites. Choice of spatial extent sizes was based on observed stand-level movements of flying squirrels released from traps (approximately 50 m, or to encompass the average gliding distance reported by Vernes 2001), with the largest plot (300 m) chosen to encompass reported home range sizes of flying squirrels (Cotton & Parker 2000). Plots were additive; larger plots included spatial features of smaller ones.

Digital inventory data were obtained from local forest companies and included all spatial features (e.g. forest polygons, openings, roads and waterbodies) around all study areas from recent provincial air photographs using provincial digitizing standards. For each forest polygon the acquired digital forest data included habitat composition, recorded as percentage cover of the primary, secondary and tertiary leading tree species, as well as polygon size (area), age (years) and height (m). To extract relevant habitat information, we converted within-polygon tree proportions to species-by-area measurements by multiplying the proportion of each species by the area for each polygon. This resulted in a tree-species-by-area measure for all GIS plots.

The forest system in northern Alberta is relatively sparse in tree diversity, so proportionally many species are the inverse of each other and autocorrelation of habitat variables is common. We wished to avoid testing uninformative hypotheses (Anderson, Burnham & Thompson 2000) of correlated variables, so we limited variable generation to those pertaining directly to our hypotheses, to those currently predicted biologically important to flying squirrels, and to those relevant to management planning using GIS. Within each plot we calculated average stand age (year), average stand height (m), percentage conifer species by area, percentage non-forest openings by area, and heterogeneity (average polygon size in m^2 , see below). Anthropogenic openings were rare relative to natural openings (e.g. low wetlands and waterbodies), so we pooled all openings into one “non-forest” category. Average polygon size was calculated as a measure of plot heterogeneity; homogeneous areas had larger average polygon size by area, heterogeneous plots had smaller average polygon size by area.

STATISTICAL ANALYSIS

We employed two main approaches to examine squirrel relative abundance according to habitat structure or type: analysis of variance and stepwise regression.

Using habitat category as a fixed effect and year as a random effect, we compared squirrel abundance among areas using a mixed-model type III ANOVA, with habitat blocked two different ways. First, based on the percentage conifer present around each trapping transect calculated separately for each of the three spatial extents, we blocked all study areas into three broad habitat categories: (i) conifer-dominated, (ii) mixed-wood, and (iii) deciduous-dominated. Deciduous areas had on average < 8% conifer, mixed-wood areas had on average 40–50% conifer, and conifer-dominated areas had > 85% conifer composition.

Secondly, we blocked all study areas into four more specific habitat types based on dominant canopy tree species. The habitat categories included (i) trembling aspen, (ii) mixed trembling aspen-spruce, (iii) white spruce and (iv) lodgepole pine. Habitat categories had > 80% composition of the leading tree species. Mixed-wood sites consisted of between 40% and 47% spruce, the remainder being trembling aspen-dominated. As spatial extent was increased, additional habitat patches were included within the GIS plots and some sites were reclassified into different habitat categories.

We used stepwise regressions to determine whether landscape composition was related to squirrel abundance independent of habitat categories. One regression was conducted for each of the three spatial extents. In all cases trapping transect was used as the experimental unit and captures per 100 trap nights was used as the dependent variable. Independent variables entered into each model included average tree height (m), average stand age (year), percentage conifer (% of area), percentage non-forest (% area) and average patch size (m^2 ; a measure of heterogeneity). Year was included as a dummy variable. The criteria probability for F to enter the model was set to 0.05, and the probability criteria of F to remove from the model was set to 0.1.

In three cases, GIS plots were not spatially independent. To achieve spatial independence, we randomly dropped one site from each of three spatially overlapping pairs (one site from the 150-m analysis, two sites from the 300-m analysis). We achieved temporal independence by sampling each study site once, sampling different sites among years, and statistically accounting for variability associated with year.

To achieve normality and reduce heteroscedasticity in the data, relative abundance of squirrels, average tree height, average stand age and average patch size were transformed using the natural log function ($\ln x + 1$). Proportion data were arcsine square-root transformed. Analyses were completed using SPSS version 8.0.

Results

In total we marked 93 individual northern flying squirrels from 32 study sites over 5935 trap nights and three mid-summer seasons of sampling. Relative abundance ranged from zero to 6.96 unique captures per 100 trap nights, with no clear trend for increased or decreased values among years or sampling regions, apart from slightly

Table 1. Captures per 100 trap nights ± SEM of northern flying squirrels in four forest types from northern and western Alberta, Canada. Captures are sorted by dominant habitat type at the 50-m spatial extent. Sample sizes are in parentheses

Year	Site	Dominant habitat type at 50-m spatial extent			
		Trembling aspen	Mixed conifer	Lodgepole pine	White spruce
1997	Athabasca	1.45 (1)	2.52 (1)	–	0.69 (1)
	Ft McMurray	2.80 (1)	0.71 (1)	–	0 (1)
	Lac La Biche	6.96 (1)	3.84 (1)	–	2.38 (1)
2001	Grande Prairie	0.28 ± 0.23 (3)	1.20 ± 0.6 (3)	–	–
	Manning	–	0.69 ± 0.34 (6)	–	0.43 ± 0.43 (2)
2003	Hinton	0.29 ± 0.15 (3)	–	1.32 ± 0.48 (3)	2.19 ± 1.22 (3)

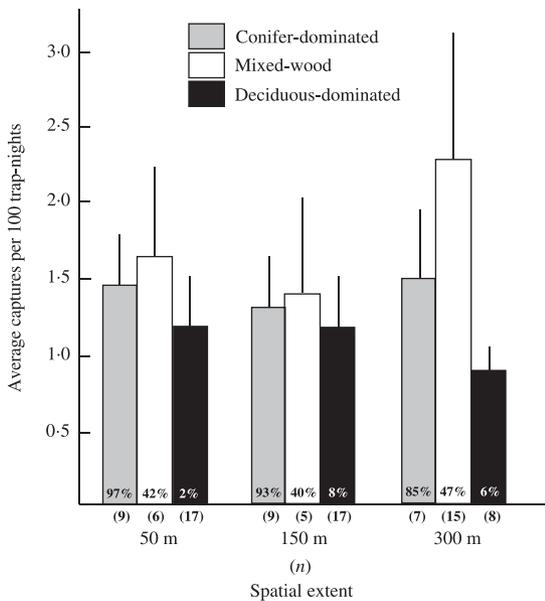


Fig. 1. Average captures per 100 trap nights of flying squirrels in three habitat categories from northern and western Alberta, Canada. As spatial extent was increased and additional habitat patches were included within larger sampling areas, some sites were reclassified into different habitat categories. Average conifer proportions for each category are listed as percentages at the bottom of each bar. Sample sizes (number of trapping transects) are in parentheses below each bar and error bars indicate SEM.

increased values at the Lac La Biche area in 1997 (Table 1). We recorded zero captures in nine of the 32 trapping transects over the three summer seasons of trapping, but these zeros appeared unrelated to local

habitat as classified within 50 m of the trapping transect (two spruce, four mixed-wood and three trembling aspen sites).

At the 300-m spatial extent there was a trend for increased squirrel abundance in mixed-wood habitat compared with conifer-dominated and deciduous-dominated habitats (Fig. 1), however this was not statistically significant (see below). We did not find any association between flying squirrel abundance and habitat at the 50-m, 150-m and 300-m spatial extents (Table 2; three-habitat comparisons). Additionally, there were no significant interactions between habitat and year at any spatial extent (all $P > 0.15$; Table 2).

Similarly, at the 300-m spatial extent there was a trend for increased squirrel abundance in mixed-wood habitat compared with trembling aspen, white spruce and lodgepole pine (Fig. 2). However, this was not statistically significant and sites were not extensively reclassified by habitat type at this level. We did not find any association between flying squirrel abundance and the four habitat categories at the 50-m, 150-m and 300-m spatial extents (Table 2; four-habitat comparisons). Additionally, there were no significant interactions between habitat and year at any spatial extent (all $P > 0.14$).

Overall regression models at 50-m and 150-m spatial extents were not significant, and consequently no environmental variables entered these models. Stepwise regression at the 300-m spatial extent was significant overall ($F_{[1,28]} = 2.1$, adjusted $r^2 = 0.20$, $P = 0.009$), with average stand height as the only significant factor predicting squirrel abundance ($t = -2.8$, $P = 0.009$; Fig. 3). Squirrel abundance was negatively associated

Table 2. Mixed-model ANOVA results comparing flying squirrel relative abundance with habitat type over three spatial extents

Spatial extent	Factors	ANOVA comparisons	
		Three habitats	Four habitats
50 m	Habitat	$F_{2,24} = 0.28$, $P = 0.77$	$F_{3,23} = 0.15$, $P = 0.93$
	Year	$F_{2,24} = 1.00$, $P = 0.46$	$F_{2,23} = 0.91$, $P = 0.49$
	Habitat × year	$F_{3,24} = 1.80$, $P = 0.16$	$F_{3,23} = 2.01$, $P = 0.14$
150 m	Habitat	$F_{2,23} = 0.24$, $P = 0.79$	$F_{3,22} = 0.14$, $P = 0.93$
	Year	$F_{2,23} = 0.96$, $P = 0.47$	$F_{2,22} = 0.98$, $P = 0.47$
	Habitat × year	$F_{3,23} = 1.60$, $P = 0.21$	$F_{3,22} = 1.72$, $P = 0.19$
300 m	Habitat	$F_{2,22} = 0.48$, $P = 0.65$	$F_{3,21} = 0.38$, $P = 0.77$
	Year	$F_{2,22} = 3.80$, $P = 0.15$	$F_{2,21} = 2.58$, $P = 0.23$
	Habitat × year	$F_{3,22} = 0.58$, $P = 0.63$	$F_{3,21} = 0.99$, $P = 0.41$

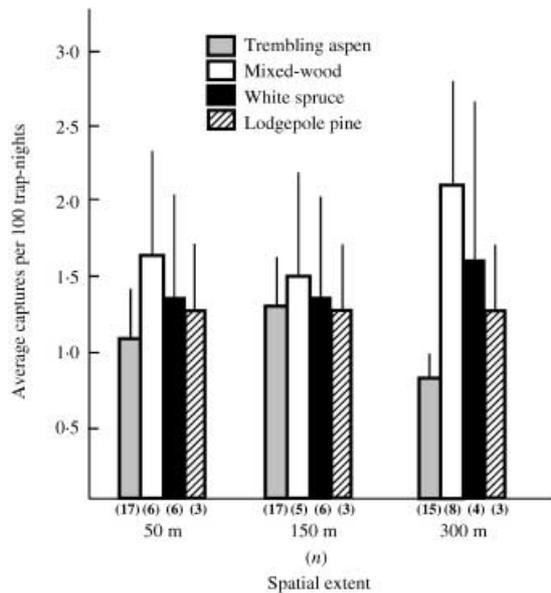


Fig. 2. Average captures per 100 trap nights of flying squirrels in four habitat categories from forests in northern and western Alberta, Canada. As spatial scale was increased and additional habitat patches were included within larger scales, some sites were reclassified into different habitat categories. Sample sizes (number of trapping transects) are in parentheses below each bar and error bars indicate SEM.

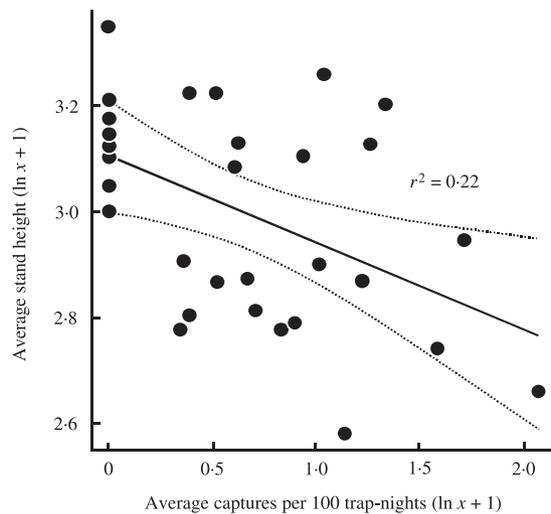


Fig. 3. Negative relationship between average stand height and flying squirrel abundance at the 300-m spatial extent from forests in northern and western Alberta, Canada. The transformed values of both variables ($\ln x + 1$) are plotted. Lines represent a best-fit linear regression with 95% confidence intervals.

with average stand height at the 300-m spatial extent. This relationship was derived from height data that ranged from 12 to 28 m.

We found little or no relationship between squirrel abundance and any of the other environmental parameters. Of note was the lack of any relationship between abundance and conifer composition (Fig. 4), a relationship that was equally disparate at all three spatial

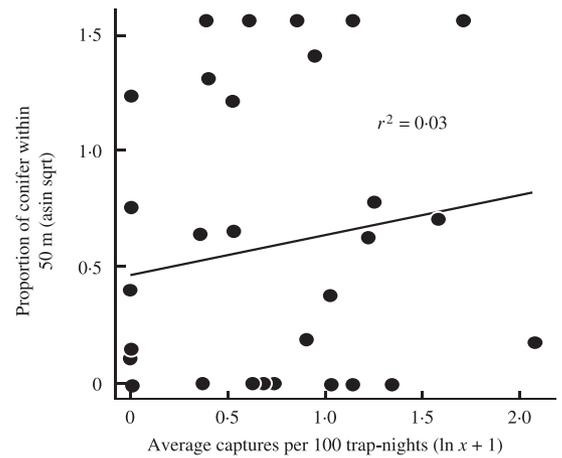


Fig. 4. There was no relationship between average conifer composition and flying squirrel relative abundance at the 50-m spatial extent from forests in northern and western Alberta, Canada. Similar relationships were also found for the 150-m and 300-m spatial extents. The transformed values of both variables [\ln abundance + 1, and arcsine square-root (asin sqrt) of conifer composition] are plotted. Solid line represents a best-fit linear regression.

extents using conifer composition data that were roughly evenly distributed between 0% and 100% among sampling areas. Similarly, we found no discernible relationship between abundance and stand age with forest age averages that ranged evenly among sites between approximately 60 and 181 years.

Discussion

Flying squirrels were found in all habitats sampled but were not significantly associated with any particular habitat type, either conifer- or deciduous-dominated, at any spatial extent. We found abundance to be completely unrelated to conifer composition, stand age (above 60 years), patch size and non-forested openings at both large and small spatial extents. Abundance was unrelated to stand height at the 50-m and 150-m spatial extents, but showed a significant negative relationship (above 12 m) at the 300-m spatial extent. Our prediction, namely that abundance would be positively related to stand age and conifer composition (Carey 1995; McDonald 1995; Smith & Nichols 2003), or other components of older forests (e.g. stand age), was not supported.

Relating flying squirrel abundance to old-growth forest in Alberta is difficult. Our results are consistent with some literature suggesting northern flying squirrel abundance is not necessarily specific to conifer habitat or related to features of older forests (Martin 1994; Rosenberg & Anthony 1992). Flying squirrel can be found in younger, second-growth forests, although it is not known whether as breeding or persistent populations. Similarly, Waters & Zabel (1995) and Pyare & Longland (2002) found no correlation between flying squirrel abundance and either snags or cavities (contrary to Smith & Nichols 2004), both prominent characteristics

of old-growth and mature forests. We expected more animals to be found in mature stands, with higher trees and larger gaps characteristic of older forests in our study areas, but response to average stand height was the reverse of our prediction and seen only at one spatial extent. Squirrel abundance in this study was similar across a continuum of habitats and stand ages, suggesting further that features other than those necessarily associated with habitat type or forest successional stage are driving flying squirrel abundance.

Increasingly, the occurrence of *G. sabrinus* is being linked to food abundance (Pyare & Longland 2002; Ransom & Sullivan 2004), specifically the abundance of truffles (Pyare & Longland 2002), the subterranean fruiting body of hypogeous fungi, identified as the primary food item in a relatively specific diet (Maser *et al.* 1986; Currah *et al.* 2000). Ransome & Sullivan (2004) present convincing evidence that food abundance is a significant, proximate mechanism driving flying squirrel abundance. However, habitat features related to food abundance are most likely to occur at a higher resolution than average stand values available from a digital forest inventory. If food is a significant proximate mechanism, then modelling the abundance of *G. sabrinus* effectively will be difficult: a clear link does not exist between hypogeous fungi and measurable habitat features or habitat types (but see Fogel 1976). Also unknown are the spatial distribution and abundance of these food items, but this is probably linked to stand-level moisture and temperature (Currah *et al.* 2000), two variables below the resolution of digital forest inventory data and typically spatially patchy within and among areas (Fogel 1976).

If proximate features affecting flying squirrel abundance show clumped or patchy spatial distributions, then this has implications for sampling techniques used to derive abundance measurements for this species used in subsequent model predictions. Spatial and temporal heterogeneity in flying squirrel capture rates (trapping 'hot spots') among and within studies has been reported (Rosenberg, Overton & Anthony 1995; Coté & Ferron 2001; Pyare & Longland 2002; present study). Pyare & Longland (2002) found correlations between capture locations and truffle diggings of northern flying squirrel in eastern Canada, and they discuss how different species of hypogeous fungi fruit at different times and persist ephemerally. They suggest that flying squirrels are exploiting microhabitats based on a combination of ephemeral fungi abundance and above-ground microhabitat characteristics that provide cover from predators, and that this results in patchy trap success over time and space. If flying squirrels are tracking ephemeral resources (Talou *et al.* 1990; Donaldson & Stoddart 1994; Pyare & Longland 2002), resulting in clumped population distributions that change over time and space, then commonly used sampling transects or grids will show 'hit and miss' capture rates. Telemetry studies relating movements to resources, i.e. foraging dispersal, will help validate

abundance data by relating capture locations to fine-scale habitat use, but because flying squirrels are nocturnal movement studies are rare (although with the advent of GPS we now know of at least four movement studies on *G. sabrinus* in North America that should become available in the near future).

Of particular interest is how our results differ from those found in Alberta by McDonald (1995). Her capture rates were similar to those reported here; however, she found positive associations between flying squirrel abundance and conifer density. Further, she found significantly more flying squirrels in older (≥ 120 years) vs. younger forests (50–65 years). Although the forest stands sampled within our study included the range of spruce composition and stand age sampled by McDonald (1995), the overall range of habitats, spatial extent surrounding plots and geographical area sampled here were greater. Habitat associations for flying squirrel appear to change significantly (i.e. were not detectable here), when examined over larger spatial extents or a greater variety of forest types at larger grain. Differences in abundance–habitat relationships reported among studies could simply reflect differences in ephemeral resource use between study areas, or a completely different functional landscape contingent on the spatial extent examined.

The performance of predictive models will depend on the vagility of the organism being studied, the predictor variables selected, and the grain and spatial extent considered (Engler, Guisan & Rechsteiner 2004). The data used here to describe landscape composition appear above the grain of perception of *G. sabrinus*. This study highlights the potential problems associated with assigning relative importance to habitat types, or landscape configurations, based on studies done at only one spatial extent or in one landscape context (Fisher, Boutin & Hannon 2005). To date, we cannot assign a habitat preference to the northern flying squirrel in Alberta, and successful management and conservation of this species will require further knowledge of within- and among-patch movement patterns of individuals with reference to key in-patch features. Efforts to predict northern flying squirrel abundance using available GIS-based digital forest inventories in North America should be dissuaded unless digital resolution is increased above general habitat polygons.

Acknowledgements

For assistance in the field we are indebted to Graham VanTighem, Tara Johnson, Kyla Johnson, Shari Clare, Kelly Sturgess, Dave McKinnon, Luke Nolan, Cris Gray and Len Peleshok. Funding for this research was provided by Weldwood of Canada (Hinton Division), Alberta Pacific Forest Industries Inc., The Alberta Research Council Inc., Ainsworth Lumber Company, Manning Diversified Forest Products and The Alberta Conservation Association. Analyses and manuscript generation were supported by a National Sciences

and Engineering Research Council of Canada scholarship awarded to M. Wheatley. In-kind support was provided by the British Columbia Ministry of Forests (Smithers and Kamloops Regions). Luc Wauters and two anonymous referees improved earlier drafts of this manuscript.

References

- Anderson, D.R., Burnham, K.P. & Thompson, W.L. (2000) Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management*, **64**, 912–923.
- Arbuckle, K.E. & Downing, J.A. (2002) Freshwater mussel abundance and species richness: GIS relationships with watershed land use and geology. *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 310–316.
- Bowman, J., Forbes, G. & Dilworth, T. (2000) Landscape context and small-mammal abundance in a managed forest. *Forest Ecology and Management*, **140**, 249–255.
- Bright, P.W. (1993) Habitat fragmentation: problems and predictions for British mammals. *Mammal Review*, **23**, 101–111.
- Carey, A.B. (1995) Sciurids in Pacific Northwest managed and old-growth forests. *Ecological Applications*, **5**, 648–661.
- Carey, A.B. (2000) Effects of new forest management strategies on squirrel populations. *Ecological Applications*, **10**, 248–257.
- Carey, A.B., Horton, S.P. & Biswell, B.L. (1992) Northern spotted owls: influence of prey base and landscape character. *Ecological Monographs*, **62**, 223–250.
- Carey, A.B., Kershner, J., Biswell, B. & Domínguez de Toledo, L. (1999) Ecological scale and forest development: squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. *Wildlife Monographs*, **142**, 1–71.
- Claridge, A.W., Cork, S.J. & Trappe, J.M. (2000) Diversity and habitat relationships of hypogeous fungi. I. Study design, sampling techniques and general survey results. *Biodiversity and Conservation*, **9**, 151–173.
- Coté, M. & Ferron, J. (2001) Short-term use of different residual forest structures by three sciurid species in a clear-cut boreal landscape. *Canadian Journal of Forest Research*, **31**, 1805–1815.
- Cotton, C.L. & Parker, K.L. (2000) Winter habitat and nest trees used by northern flying squirrels in subboreal forests. *Journal of Mammalogy*, **81**, 1071–1086.
- Currah, R.S., Smreciu, E.A., Lehesvirta, T., Niemi, M. & Larsen, K.W. (2000) Fungi in the winter diets of northern flying squirrels and red squirrels in the boreal mixedwood forest of northeastern Alberta. *Canadian Journal of Botany*, **78**, 1514–1520.
- Donaldson, R. & Stoddart, M. (1994) Detection of hypogeous fungi by Tasmanian bettong. *Journal of Chemical Ecology*, **20**, 1201–1207.
- Engler, R., Guisan, A. & Rechsteiner, L. (2004) An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *Journal of Applied Ecology*, **41**, 263–274.
- Fisher, J.T., Boutin, S. & Hannon, S.J. (2005) The protean relationship between boreal forest landscape structure and red squirrel distribution at multiple spatial scales. *Landscape Ecology*, in press.
- Fogel, R. (1976) Ecological studies of hypogeous fungi. II. Sporocarp phenology in a western Oregon Douglas fir stand. *Canadian Journal of Botany*, **54**, 1152–1162.
- Gibson, L.A., Wilson, B.A., Cahill, D.M. & Hill, J. (2004) Spatial prediction of rufous bristlebird habitat in a coastal heathland: a GIS-based approach. *Journal of Applied Ecology*, **41**, 213–223.
- Hatten, J.R. & Paradzick, C.E. (2003) A multiscaled model of southwestern willow flycatcher breeding habitat. *Journal of Wildlife Management*, **67**, 774–788.
- Holloway, G.J., Griffiths, G.H. & Richardson, P. (2003) Conservation strategy maps: a tool to facilitate biodiversity action planning illustrated using the heath fritillary butterfly. *Journal of Applied Ecology*, **40**, 413–422.
- Ireland, R.J. (1980) *Checklist of the Mosses of Canada*. Canadian Botanical Association, National Museums of Canada, Ottawa, Canada.
- Jaberg, C. & Guisan, A. (2001) Modelling the distribution of bats in relation to landscape structure in a temperate mountain environment. *Journal of Applied Ecology*, **38**, 1169–1181.
- Jeganathan, P., Green, R.E., Norris, K., Vogiatzakis, I.N., Bartsch, A., Wotton, S.R., Bowden, C.G.R., Griffiths, G.H., Pain, D. & Rahmani, A.R. (2004) Modelling habitat selection and distribution of the critically endangered Jerdon's courser *Rhinoptilus bitorquatus* in scrub jungle: an application of a new tracking method. *Journal of Applied Ecology*, **41**, 224–237.
- Johnson, C.J., Parker, K.L. & Heard, D.C. (2001) Foraging across a variable landscape: behavioural decisions made by woodland caribou at multiple spatial scales. *Oecologia*, **127**, 590–602.
- Johnson, C.J., Seip, D.R. & Boyce, M.S. (2004) A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. *Journal of Applied Ecology*, **41**, 238–251.
- Kershaw, L.J., Pojar, J. & Mackinnon, A. (1998) *Plant of the Rocky Mountains*. Lone Pine Publishing, Edmonton, Canada.
- Kotliar, N.B. & Wiens, J.A. (1990) Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos*, **59**, 253–260.
- Levin, S.A. (1992) The problem with pattern and scale in ecology. *Ecology*, **73**, 1943–1967.
- McDonald, L. (1995) Relationships between northern flying squirrels and stand age and structure in aspen mixedwood forests in Alberta. *Relationships Between Stand Age, Stand Structure, and Biodiversity in Aspen Mixedwood Forests in Alberta* (ed. J. B. Stelfox), pp. 227–240. Jointly published by Alberta Environmental Centre (AECV95-R1), Vegreville, Canada and The Canadian Forest Service (Project No. 0001A), Edmonton, Canada.
- Mackey, B.G. & Lindenmayer, D.B. (2001) Towards a hierarchical framework for modelling the spatial distribution of animals. *Journal of Biogeography*, **28**, 1147–1166.
- Martin, K.J. (1994) *Movements and habitat characteristics of northern flying squirrels in the central Oregon Cascades*. MSc Thesis. Oregon State University, Corvallis, OR.
- Maser, C., Maser, Z., Witt, J. & Hunt, G. (1986) The northern flying squirrel: a mycophagist in southwest Oregon. *Canadian Journal of Zoology*, **64**, 2086–2089.
- Maser, C., Trappe, J.M. & Nussbaum, R.A. (1978) Fungal–small mammal interrelationships with emphasis on Oregon coniferous forests. *Ecology*, **59**, 799–809.
- Moss, E.H. (1994) *Flora of Alberta*, 2nd edn. University of Toronto Press, Toronto, Canada.
- Nelson, L. Jr & Clark, F.W. (1973) Correction for sprung traps in catch/effort calculations of trapping results. *Journal of Mammalogy*, **54**, 295–298.
- North, M., Trappe, J.M. & Franklin, J. (1997) Standing crop and animal consumption of fungal sporocarps in Pacific Northwest forests. *Ecology*, **78**, 1543–1554.
- Osborne, P.E., Alonso, J.C. & Bryant, R.G. (2001) Modelling landscape-scale habitat use using GIS and remote sensing: a case study with great bustards. *Journal of Applied Ecology*, **38**, 458–471.
- Pearce, J.L., Cherry, K., Drielsma, M., Ferrier, S. & Whish, G. (2001) Incorporating expert opinion and fine-scale vegetation

- mapping into statistical models of faunal distribution. *Journal of Applied Ecology*, **38**, 412–424.
- Pyare, S. & Longland, W.S. (2002) Interrelationships among northern flying squirrels, truffles, and microhabitat structure in Sierra Nevada old-growth habitat. *Canadian Journal of Forest Research*, **32**, 1016–1024.
- Ransome, D.B. & Sullivan, T.P. (2003) Population dynamics of *Glaucomys sabrinus* and *Tamiasciurus douglasii* in old-growth and second-growth stands of coastal coniferous forest. *Canadian Journal of Forest Research*, **33**, 587–596.
- Ransome, D.B. & Sullivan, T.P. (2004) Effects of food and den-site supplementation on populations of *Glaucomys sabrinus* and *Tamiasciurus douglasii*. *Journal of Mammalogy*, **85**, 206–215.
- Reunanen, P., Nikula, A., Mönkkönen, M., Hurme, E. & Nevala, V. (2002) Predicting occupancy for the Siberian flying squirrel in old-growth forest patches. *Ecological Applications*, **12**, 1188–1198.
- Rodríguez, A. & Andrén, H. (1999) A comparison of Eurasian red squirrel distribution in different fragmented landscapes. *Journal of Applied Ecology*, **36**, 649–662.
- Rosenberg, D.K. & Anthony, R.G. (1992) Characteristics of northern flying squirrel populations in young second- and old-growth forests in western Oregon. *Canadian Journal of Zoology*, **70**, 161–166.
- Rosenberg, D.K., Overton, W.S. & Anthony, R.G. (1995) Estimation of animal abundance when capture probabilities are low and heterogeneous. *Journal of Wildlife Management*, **59**, 252–261.
- Rowe, D.K., Shankar, U., James, M. & Waugh, B. (2002) Use of GIS to predict effects of water level on the spawning area for smelt, *Retropinna retropinna*, in Lake Taupo, New Zealand. *Fisheries Management and Ecology*, **9**, 205–216.
- Rushton, S.P., Lurz, P.W.W., Fuller, R. & Garson, P.J. (1997) Modelling the distribution of the red and grey squirrel at the landscape scale: a combined GIS and population dynamics approach. *Journal of Applied Ecology*, **34**, 1137–1154.
- Rushton, S.P., Lurz, P.W.W., Gurnell, J. & Fuller, R. (2000) Modelling the spatial dynamics of parapoxvirus disease in red and grey squirrels: a possible cause of the decline in the red squirrel in the UK? *Journal of Applied Ecology*, **37**, 997–1012.
- Rushton, S.P., Ormerod, S.J. & Kerby, G. (2004) New paradigms for modelling species distributions? *Journal of Applied Ecology*, **41**, 193–200.
- Smith, W.P. & Nichols, J.V. (2003) Demography of the Prince of Wales flying squirrel, an endemic of southeastern Alaska temperate rain forest. *Journal of Mammalogy*, **84**, 1044–1058.
- Smith, W.P. & Nichols, J.V. (2004) Ecological correlates of flying squirrel microhabitat use and density in temperate rainforests of southeastern Alaska. *Journal of Mammalogy*, **85**, 663–674.
- Strong, W.L. (1992) *Ecoregions and Ecodistricts of Alberta*, Vol. 1. Alberta Forestry, Lands and Wildlife, Land Information Services Division, Resource Information Branch, Government of Alberta, Edmonton, Canada.
- Suárez-Seoane, S., Osborne, P.E. & Alonso, J.C. (2002) Large scale habitat selection by agricultural steppe birds in Spain: identifying species–habitat responses using generalized additive models. *Journal of Applied Ecology*, **39**, 755–771.
- Talou, T., Gaset, A., Delmas, M., Kulifaj, M. & Montant, C. (1990) Dimethyl sulfide: the secret for black truffle hunting by animals? *Mycological Research*, **94**, 277–278.
- Turchin, P. (1996) *Movement and Spatial Population Dynamics*. John Wiley, New York, NY.
- Turner, M.G. & Gardner, R.H. (1991) *Quantitative Methods in Landscape Ecology: An Introduction*. Springer-Verlag, New York, NY.
- Verner, J., Morrison, M.L. & Ralph, C.J. (1986) *Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates*. University of Wisconsin Press, Madison, WI.
- Vernes, K. (2001) Gliding performance of the northern flying squirrel (*Glaucomys sabrinus*) in mature mixed forest of eastern Canada. *Journal of Mammalogy*, **82**, 1026–1033.
- Waters, J.R. & Zabel, C.J. (1995) Northern flying squirrel densities in fir forests of northeastern California. *Journal of Wildlife Management*, **59**, 858–866.

Received 11 July 2004; final copy received 10 February 2005

Editor: Steve Rushton